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# ON REVERSIBLE TRANSFORMABILITY OF ALLELOMORPHS

H. TERA0

THE IMPERIAL AGRICULTURAL EXPERIMENT STATION, TOKYO, JAPAN

IN genetical studies of variegation in plants, the fact has been observed occasionally that with a certain frequency a dominant allelomorph occurs in the corresponding recessive homozygote (De Vries,<sup>1</sup> Correns,<sup>2</sup> and Emerson<sup>3</sup>). In this paper the author presents a new instance of a similar phenomenon, which it is hoped may throw additional light on the subject.

In certain pedigree cultures of the rice plant, *Oryza sativa* L., there happened to occur in 1912 families containing besides ordinary fertile plants a number of sterile plants. These sterile plants were normal in their growth, but showed a considerable barrenness at the ripening season. Some of them yielded no seed whatsoever, others bore a small number of normal seeds, and very few were mosaic forms with higher fertility. These families, two in number, each belonging to a different variety, were derived from single plants of the former generation, and were very uniform in other characters. From them the experiment was started.

The rice plant, being a self-pollinated species, is convenient material for breeding experiments. Although the experiments in this investigation were made largely from open-pollinations, the results obtained were always similar to those from experiments in which plants were artificially protected against accidental natural crossing.

The observations of 1912 and 1913 are shown in summarized form in Tables I and II, *a* and *b*, and point to the following conclusions. Sterility behaves as a simple re-

<sup>1</sup> De Vries, H., "Die Mutationstheorie," Bd. I, 1901, pp. 489-511; "Species and Varieties, their Origin by Mutation," 1905, pp. 309-339.

<sup>2</sup> Correns, C., *Berichte der Deutschen Botanischen Gesellschaft*, Bd. 28, 1910, pp. 418-434.

<sup>3</sup> Emerson, R. A., *AMERICAN NATURALIST*, Vol. 48, 1914, pp. 87-115; *Genetics*, Vol. 2, 1917, pp. 1-35.

cessive to fertility, and the seeds resulting from partial fertility of sterile plants again give segregating families. In Family *A*, which shows an exceedingly slight fertility of sterile plants, the segregation ratio in the offspring derived from fertile individuals is quite close to expectation, but in Family *B* which shows a considerably higher grade of partial fertility of sterile plants, the progeny of fertile individuals exhibit considerable deviations from the expected segregation ratio.

TABLE I  
THE SEGREGATING FAMILIES, *A* AND *B*, IN 1912

Fam.	Segregation					Partial Fertility of Sterile Plants		
	Fertile Plants	Sterile Plants	Total No. of Ind.	Steriles %	Ratio per 4		Total No. of Spikelets	Fertile Spikelets
					D	R		No.
<i>A</i> . . . .	36	13	49	26.53	2.94	1.06	ca. 9,000	2
<i>B</i> . . . .	105	25	130	19.23	3.23	0.77	14,941	434

TABLE II  
THE FAMILIES DERIVED FROM FAMILIES *A* AND *B*  
(*a*) *The Progeny of the Fertile Plants*

Family in 1912	No. of Families			Ratio per 3		Segregating Families			
	Uniformly Fertile	Segregating	Total	Uniformly Fertile Families	Segregating Families	Fertile Plants	Sterile Plants	Total Number Individuals	Steriles %
<i>A</i> . . . .	10	22	32	0.94	2.06	1,068	346	1,414	24.46
<i>B</i> . . . .	41	64	105	1.17	1.83	4,874	1,301	6,175	21.06

(*b*) *The Progeny of the Seeds on the Sterile Plants*

Family in 1912	Number of Families	Fertile Plants	Sterile Plants	Total Number of Individuals	Steriles %
<i>A</i> . . . . .	2	2	0	2	0.00
<i>B</i> . . . . .	24	401	115	516	22.29

These facts may be interpreted by the following hypothesis. The dominant and the recessive types concerned are assumed to be transformed by certain unknown causes into the other allelomorph. The recessive allelomorph which has made its appearance in Families *A* and *B* is assumed to have originated in the preceding

generation by the transformation of the dominant allelomorph. This recessive state of the hereditary substance, however, has a tendency to revert into the original dominant state. Such reversion is especially likely to occur in vegetative cells, where each recessive allelomorph seems to be able to revert independently. Consequently, in recessive homozygotes the reversion generally will produce heterozygotic cells, either one of the two recessive allelomorphs being changed into the dominant. The heterozygotic cells thus formed will give rise to partial fertility in otherwise sterile plants. Again, the recessive allelomorph in heterozygotic cells may be subject to similar reversion, and such reversion may occur both in the heterozygotic cells of sterile plants and in normal heterozygotes. Here, however, heterozygotic cells will be transformed into dominant homozygotic cells without visible effect on the plant concerned. The consequence of this reversion in the next generation will be that the proportion of the dominant segregates may exceed the theoretically expected figure. Finally, it may be assumed that between Families *A* and *B* there exists a difference in the reverting tendency of the recessive allelomorph, which necessarily will effect the differences in both the intensity of partial fertility of sterile plants and the deviations in the segregation ratio.

In Table III the segregating families derived from the fertile plants of Family *B* are classified according to the magnitudes of the deviations in terms of probable errors. The true percentage for the recessive is assumed, in the one case as 25 per cent. (the Mendelian ratio), and in the other case as 21 per cent. (an arbitrary number). In comparing the two different frequency distributions made in this manner with the theoretical frequency distribution, it is observed that while the frequency distribution of the deviations from 25 per cent. shows a considerable discrepancy from the theoretical, the latter fits the frequency distribution of the deviations from 21 per cent. rather closely, the goodness of fit being  $P = 0.915$ . Consequently, the *ca.* 4 per cent. deficiency of recessive segre-

gates is a normal expectation and not an experimental error.

TABLE III

THE FREQUENCY DISTRIBUTION OF THE DEVIATIONS IN THE SEGREGATION RATIOS IN THE GROUP OF 64 SEGREGATING FAMILIES DESCENDED FROM FAMILY *B* OF THE YEAR 1912

Dev. /P.E.	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	Total
Experimental frequency (I)....	1	7	14	17	15	6	4					64
Experimental frequency (II) ...		1	2	11	19	14	10	5	2			64
Expectation .....	0.2	1.2	4.3	10.3	16.0	16.0	10.3	4.3	1.2	0.2		64.0

Note: In the experimental frequency (I) the true percentage for recessives is taken as 25 per cent., and in (II) as 21 per cent.

Such an aberrant segregation ratio seems to be a constant tendency all through the generations descended from Family *B*. This is shown in Table IV in which the experiments in the years from 1912 to 1915 are summarized.

TABLE IV

THE ABERRANT SEGREGATION-RATIOS OBTAINED IN THE YEARS 1912-1915

Years	No. of Fams.	Parent-plants	No. of Inds.	Fertiles	Steriles	Ster. %	Dev. %	P.E. %	D./P.E.
1912 .....	1	Fertile	130	105	25	19.23	5.77	2.55	2.3
1913 .....	64	"	6,175	4,874	1,301	21.06	3.94	0.37	10.6
1914 .....	10	"	1,560	1,207	353	22.63	2.43	0.74	3.3
1915 .....	53	"	4,696	3,732	964	20.52	4.48	0.47	9.5
Total....	128		12,561	9,918	2,643	21.04	3.96	0.26	15.2
1913 .....	24	Sterile	516	401	115	22.29	2.71	1.21	2.2
1914 .....	34	"	994	779	215	21.63	3.37	0.93	3.6
1915 .....	19	"	684	522	162	23.68	1.32	1.12	1.2
Total....	77		2,194	1,702	492	22.43	2.57	0.62	4.1

Again, in regard to the intensity of partial fertility of sterile plants, the descendants of Families *A* and *B* exhibited respectively relations similar to those seen in 1912. (Family *A* was not traced after 1913.) A count of fertile spikelets on sterile plants descending from Family *B* was made in 1914 on 281 plants bearing a total of 101,412 spikelets. In this count the number of fertile spikelets was 3,857, corresponding to 3.78 per cent. of the total number of spikelets. The latter figure may be regarded as the average fertility of sterile plants in the progeny of Family *B*.

The fertile spikelets of sterile plants are generally scattered at random over the panicle, and each fertile spikelet may be regarded as representing a separate case of reversion; but in mosaic forms which show higher fertility and are of rarer occurrence, the reversion may have taken place in earlier stages of plant development, resulting in larger fertile sections. Consequently, when the count of fertile spikelets is made with only the first type of sterile plants, a more correct value for the frequency of reversion may be obtained. The result of such a count on 902 panicles containing 93,635 spikelets is 1,858 fertile spikelets, *i. e.*, 1.98 per cent. of the total number of spikelets.

The mosaic forms appear in several different grades of partial fertility. In a panicle either one or more branches or even one half of the panicle can be highly or entirely fertile, the remaining part being absolutely or nearly absolutely sterile. Similarly, in a single plant some whole panicles can be entirely or highly fertile while others are of the ordinary grade of partial fertility. Furthermore, similar mosaic conditions were also observed in single flowers of sterile spikelets. While all six anthers of a sterile spikelet generally bear none or but few pollen grains, occasionally flowers appear in which certain anthers contain a considerable number of pollen grains of normal appearance and others show the ordinary state of sterility. Hence it may be assumed that the reversion can take place at any stage of plant development.

The partial homozygosity of heterozygotes, corresponding to the partial fertility of sterile plants, may be estimated in the following way. Assuming that the possibility of reversion at any stage of a plant's life, similar to that observed above, may also occur in heterozygotic cells, then we may distinguish for convenience two different types of reversions; there is the reversion which will cause partial homozygosity within a single flower, and the reversion which will produce an entirely homozygotic spikelet or larger homozygotic sectant. Suppose then that the latter reversion will give to the heterozygote

homozygotic (AA) spikelets in any part "x" of the total number of spikelets which is taken as a unit, and again that in the remaining  $(1 - x)$  part of the total number of spikelets, the other type of reversion will occur, turning some part "y" of the whole generative tissue taken as a unit from the Aa state to the AA state. For simplicity, however, we may substitute "x" for "y" in the above relation, because it seems presumable that a similar probability of reversion may exist constantly all through the plant life. Such a plant will have the following constitution in regard to the generative tissue:

$$x(AA) + (1 - x)[x(AA) + (1 - x)(Aa)].$$

As the result of self-pollination, the progeny of such a parent plant will show the constitution:

$$x(AA) + (1 - x)\left[\frac{1}{4}(1 + x)^2(AA) + \frac{1}{2}(1 - x^2)(Aa) + \frac{1}{4}(1 - x)^2(aa)\right].$$

Applying arbitrary values to "x" in this formula, we shall get numerical relations among segregates. In Table V the results of such calculation are compared with results obtained by the experiments in 1913-1915. Thus we may find the average partial homozygosity of heterozygotes around 4 to 6 per cent., the average partial fertility of sterile plants being, as was already shown, *ca.* 4 per cent.

TABLE V  
CALCULATIONS ON DATA OF TABLE IV

$x\%$	(AA + Aa)	aa	AA	Aa
4 % .....	77.88 %	22.12 %	38.74 %	61.53 %
5 % .....	78.57	21.43	39.69	60.31
6 % .....	79.24	20.76	40.89	59.11
Observation, No. of Inds.....	9,918	2,643	94	135
Percentage.....	78.96 %	21.04 %	41.05 %	58.95 %

It has also been noticed that the sterility concerned is associated with an abnormality represented by the behavior of chlorophyll at the ripening of seeds. While, at the ripening season, the chlorophyll in the fertile sections of the mosaic forms turns to yellow just as in ordinary fertile plants, the chlorophyll in the sterile sections still

remains green. The fertile spikelets occurring in a small number on the otherwise sterile panicle appear on ripening as yellow spots scattered among green spikelets; the plants with both sterile and fertile panicles appear in the fall also as mosaic forms with green and yellow leaves. This feature of the sterile plants is in direct contrast to the behavior of the mosaic plants with the variegated and the entirely green leaves studied by De Vries and Correns.

The observations in the foregoing pages seem to parallel those made by the authors cited at the beginning of this paper. In the present investigation, however, there was observed also the transformation of allelomorphs in the opposite direction, that is, the transformation of the dominant allelomorph into the recessive allelomorph, something scarcely mentioned in the investigations referred to above. The observations in this regard were in brief as follows.

In the first place, the spontaneous occurrence of segregating families was observed again among the descendants of the families which had proved in the experiments already described to be constantly fertile. This suggests, just as did the occurrence in Family *A* and Family *B* in 1912, the probability of the AA cell changing into the Aa cell.

In the second place, a constant tendency of the dominant allelomorph to be transformed into the recessive allelomorph was observed in certain strains. In 1913, special attention was paid to such segregating families in which the excess of recessive segregates over the theoretical expectation was particularly high. Although, as already noted, the variation among the segregating families in 1913 with regard to the deviations from the recessive proportion might possibly have arisen from experimental errors associated with a certain probability of allelomorphic reversion from recessive to dominant, yet it was deemed not impossible that the very considerable excess of recessives exhibited by certain families might be caused by other reasons. This point was seemingly de-



cided by the experiment made with Family *B*80 in 1913 (Table VI), since in this family there was noticed a constant tendency toward the allelomorphic transformation under consideration.

TABLE VI

THE SEGREGATION OF FAMILY *B*/80 AND ITS DESCENDANTS

Year	No. of Families	Parent-plants	No. of Individuals	Fertile Plants	Sterile Plants	Recessives	Deviation of Recessives	P. E.
1913. . .	1	Fertile	99	69	30	30.30%	+ 5.30%	2.95%
1914. . .	10	"	1,020	727	293	28.73	+ 3.73	0.91
1915. . .	5	"	435	309	126	28.89	+ 3.89	1.40
1916. . .	98	"	11,013	7,832	3,181	28.88	+ 3.88	0.28
Total. .	114	Fertile	12,567	8,937	3,630	28.89%	+ 3.89%	0.26%
1914 ( <i>a</i> ). .	16 <sup>1</sup>	Sterile	199	147	52	23.62%	- 1.38%	2.04%
1914 ( <i>b</i> ). .	13 <sup>1</sup>	Sterile	100	5	95	95.00%	+70.00%	2.92%
1915. . .	59 <sup>2</sup>	"	548	32	516	94.16	+69.16	1.25
1916. . .	120 <sup>2</sup>	"	1,436	99	1,337	93.11	+68.11	0.77
Total. .	192 <sup>3</sup>	Sterile	2,084	136	1,948	93.47%	+68.47%	0.64%

<sup>1</sup> Derived from the family in 1913, *i. e.*, Family *B*/80.

<sup>2</sup> Derived from the group (*b*) in 1914.

<sup>3</sup> Excluding the group (*a*) in 1914.

In Table VI there is beside the *ca.* 4 per cent. excess of recessives in the families derived from fertile parents, a remarkable excess of recessives in the families descended from the sterile parents in the group (*b*) in 1914. The sterile plant of this type could not be distinguished from those which, as was shown in Table IV, gave segregating families with an excess of dominants in the intensity of the partial fertility as well as in the behavior of chlorophyll at the ripening of the seeds. Consequently, it may be presumed that although these two types of sterile plants have the same genetical constitution originally, the dominant allelomorphs resulting from the reversion of their recessive allelomorphs are of different stabilities in the dominant state; that is, in the first type of sterile plants such dominant allelomorphs are very easily re-transformed into the recessive state, while in the second type the corresponding dominant allelomorphs tend to remain in the reverted condition.

Corresponding to the excess of recessive segregates, a deficiency of dominant homozygotes among dominant segregates was also noticed. Among 153 families derived from fertile plants in the experiment above mentioned, 40 families were uniformly fertile, the remaining 113 families showing segregation. The former, therefore, is 26.14 per cent. of the total number of families, and shows 7.19 per cent deficiency from the theoretically expected percentage, 33.33 per cent., the probable error being  $\pm 2.68$  per cent.

In conclusion it may be stated that the allelomorphs concerned in this investigation are probably subject to reversible transformations, and that the probable frequency of the allelomorphic transformation may be practically constant in a certain strain, and possibly may be different in different strains. As to the conditions under which such allelomorphic transformations take place, nothing is yet certain except that these conditions are of a hereditary nature. The manner in which different intensities of allelomorphic transformations are inherited will be the subject of further investigation.

A word may be added here regarding the conception of dominance and recessiveness. Bateson's theory of "presence and absence of factors" is sometimes understood in the sense that the dominant allelomorph is regarded as due to the real presence of an hereditary material unit which is absent in the recessive allelomorph. Such a conception is not in full accordance with the idea of the reversible transformability of allelomorphs as described in this investigation. There is another possibility of the nature of allelomorphs. The dominant and the recessive allelomorphs may be supposed to represent two alternative conditions or phases of a single hereditary substance, somewhat resembling the chemical conception of polymerization. Consequently, the interchangeability between the dominant and recessive allelomorphs is not improbable theoretically.